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Research Article

Energetic metabolism and condition indices in native versus invasive common waxbills

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Abstract

Invasive alien species (IAS) pose a serious threat to global biodiversity, and unravelling the mechanisms driving their expansion across new ranges remains an important challenge for ecosystem conservation. Assessing similarities and differences in species' traits and phenotypic fitness proxies between native and invasive populations can show how species may have locally adjusted in the new areas and their capacity to expand further. Here, we compare basal metabolic rates (BMR), body and nutritional condition (based on feather proxies) and body size between native (South Africa) and invasive (northern and southern Portugal) common waxbills (*Estrilda astrild*). As expected, given prevailing ambient temperatures - similar between South Africa and northern Portugal but hotter in southern Portugal - our results showed that mass-independent BMR was similar between individuals from South Africa and northern Portugal, but lower in individuals from warmer southern Portugal. However, contrary to our expectations based on the enemy release hypothesis, feather density was higher in South African birds, challenging the assumption that invasive populations outperform their native counterparts. Additionally, feather growth rates trade-off with feather quality in the introduced populations, indicating that they may face energetically challenging environments in their invaded range. Common waxbills in South Africa were larger than those in Portugal, but further analyses showed that these size differences between native and invasive birds may be influenced by introduction history rather than ecological factors alone. This study highlights the importance of considering both native and invaded ranges when studying invasive species and provides insights into the strategies used by waxbills to thrive in different environments.

Key words: Basal metabolic rate, body condition, body size, common waxbills, enemy release hypothesis, invasive species, nutritional condition

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Introduction

Invasive alien species (IAS) significantly threaten global biodiversity (Pyšek et al. 2012; Doherty et al. 2016; Mollot et al. 2017). They are responsible for ca. 60% of global species extinctions, and their economic cost has increased fourfold every decade, with an estimated cost of US$423 billion in 2019 (IPBES 2023).

Understanding the mechanisms that drive the expansion of populations introduced beyond their native range is critical for ecosystem conservation (Louppe et al. 2018). The success of invasions depends on a combination of location-, species- and population-specific characteristics, as well as the particulars of the introduction event, such as the number of individuals released and the frequency of introductions (Lockwood et al. 2005; Redding et al. 2019). Once established, non-native populations may face significant selective pressures as they expand their invasive range, and their fitness in novel environments can be maintained through phenotypic plasticity, adaptation, or both (Whitney and Gabler 2008; Buswell et al. 2011; Mathys and Lockwood 2011; Gleditsch and Sperry 2019). Phenotypic changes, such as those promoting dispersal or adjusting to new climates, can be advantageous for invasive species (Phillips et al. 2010; Berthouly-Salazar et al. 2012, 2013, Cardilini et al. 2016; Louppe et al. 2018). The study of emerging phenotypic differences between native and invasive populations can thus shed light on the mechanisms by which species can establish in new areas (Cardilini et al. 2016).

Studies often find that invasive populations perform better in their introduced habitats than populations in their native ranges (Drenovsky et al. 2008; Woods and Sultan 2022). A main hypothesis put forward to explain these findings is that individuals in invasive populations may have more energy available to invest in growth, reproduction, and survival as they are freed from the co-evolved predators, competitors, and pathogens they encounter across their native range (Keane and Crawley 2002; Torchin et al. 2003; Taniguchi et al. 2017). However, studies comparing the performance of native and invasive populations are far from uniform in their conclusions and show considerable variability between taxa (Davidson et al. 2011). For example, animal invaders often show smaller differences in performance between native and invasive populations than invasive plants (Parker et al. 2013; Lima Junior et al. 2015). Moreover, it is often unclear whether such differences in performance are because of ecological factors, such as the release of natural enemies, or anthropogenic factors, such as the selective introduction of larger individuals for transport and introduction (Miller et al. 2002). Additionally, there is increasing evidence that species with greater intraspecific variability may be more successful invaders because such variability may reflect the capacity to respond flexibly to novel or fluctuating environmental conditions (González-Suárez et al. 2015; Forsman and Wennersten 2016; Zhao et al. 2019). Historically, invasion biology has focused on mean species traits as predictors of invasion success (Hayes and Barry 2008), however, incorporating measures of trait variability could provide equally important insights (González-Suárez et al. 2015). Therefore, research examining intraspecific variation and its underlying causes is essential for developing more robust predictive models of invasion success that integrate both species-level mean trait data and explicit measures of intraspecific variability (Haubrock et al. 2024; Liu et al. 2025).

While progress has been made in identifying the ecological, behavioural, and genetic factors underpinning species invasions (Bock et al. 2015), the study of functional traits (i.e., those important for the performance and fitness of a species; Chown and McGeoch (2023)) that contribute to invasion success, is only beginning to develop. For example, Sibilia et al. (2018) found that the colder temperatures experienced by harlequin bugs (*Murgantia histrionica*) in the northern United States of America (USA) resulted in smaller, darker bugs that were better at thermoregulating than native Central American populations. Of the functional traits studied in invasive populations, those related to physiology remain the least understood (Kelley 2014; Lennox et al. 2015), yet these traits are critical for determining how invaders cope with

novel thermal or energetic constraints (Lennox et al. 2015). For instance, Louppe et al. (2018) found that differences in metabolic rates between central and expanding edge populations of invasive African clawed frogs (*Xenopus laevis*) resulted in distinct phenotypes in which frogs from the periphery were able to allocate more energy to locomotor performance. However, an important research gap persists in comparing these traits between native and invasive ranges, especially for endotherms. Such comparisons could provide insights into how the species has locally adjusted in the new areas, whether the species is thriving in the new environment and whether it has the capacity to expand further (Phillips and Shine 2005; van Kleunen et al. 2010).

Birds have served as prominent models for understanding the dynamics of invasive species, yet studies investigating the physiological responses underpinning their successful establishment remain limited (Blackburn et al. 2009). Existing studies contrasting native and invasive ranges have primarily focused on morphological changes (e.g. Berthouly-Salazar et al. 2012; Le Gros et al. 2016; Valentin et al. 2018), but the physiological changes accompanying invasion remain largely unexplored. Incorporating measurements of energetic metabolism, assessing body size and condition, and examining feather characteristics as indicators of nutritional condition could improve our understanding of avian invasion performance. The basal metabolic rate (BMR) of a species represents its minimum rate of energy expenditure and is an important aspect of an organism's energy budget (McNab 2012; Nilsson and Nilsson 2016). The BMR is individually repeatable yet plastic, for example, decreasing during periods of low food availability to conserve energy, and increasing in colder conditions in relation to thermoregulation (McKechnie 2008). Assessing BMR differences between native and invasive populations can, therefore, enhance our understanding of the energetic demands faced by non-native organisms in new environments. Body size can be a reliable proxy for developmental conditions, as small individuals are often energetically constrained during growth (Meillère et al. 2017; Kraft et al. 2019). Body condition reflects an individual's energetic or nutritional state and indicates their ability to meet their energetic requirements (Peig and Green 2009). Finally, feather characteristics, such as feather density or feather growth bar widths (GBW), can provide information on the conditions experienced by individuals during moult. The moulting period is crucial because it is energetically demanding, and plumage quality can affect individual performance until the next moulting cycle (Dawson et al. 2000). These metrics are commonly used proxies in ecological studies and are known to reflect, at least partially, environmental conditions and resource availability (BMR: Wiersma et al. 2007; Body Condition: Peig and Green 2009; Body Size: Kraft et al. 2019; Feather Density: Pap et al. 2020).

Here, we examined physiological and morphological differences between native and invasive populations of the common waxbill (*Estrilda astrild*). The common waxbill is a small sub-Saharan estrildid finch (7–9 g) that has become invasive and is widely distributed globally because of the global pet trade (Stiels et al. 2011; Cardoso and Reino 2018). Introductions of common waxbills to non-native regions such as Brazil (da Silva et al. 2018), the Hawaiian and Caribbean islands, and Europe, particularly in parts of Iberia (Reino and Silva 1998), make them an ideal study system. In Iberia, the northern populations represent the northernmost distribution limit of the species, and they experience a colder and less predictable climate than most of their native range (Stiels et al. 2011). Invasive waxbills in Portugal strategically regulate their BMR, lowering it in winter to conserve energy and adjusting it to ambient temperatures in summer to avoid overheating (Sentís et al. 2025). However, no studies have investigated

the physiological and morphological differences of this species between invasive and native ranges. Thus, a comprehensive joint examination of these traits may improve our understanding of common waxbills' energetic and nutritional status in their invaded range compared with their native range, which may indicate how well they have adjusted to the new environment and outperform (or not) native common waxbills.

Our study compared BMR, body size, and nutritional and body condition of common waxbills between their native range in South Africa and their invasive range in Portugal. We captured and measured waxbills from three sites: two in Portugal (northern and southern) and one in South Africa. Under the enemy release hypothesis, we predicted that invasive waxbills would be larger and exhibit higher body mass and nutritional condition than their native counterparts. Additionally, we expected common waxbill populations to adjust their BMR to local environmental conditions. Ambient temperatures during the fieldwork months are similar in South Africa and northern Portugal but hotter in southern Portugal (suppl. material 1: fig. S1). We therefore predicted comparable BMRs for waxbills in South Africa and northern Portugal and a lower BMR in birds from southern Portugal, consistent with the negative correlation between ambient temperature and BMR reported for the species in summer in Portugal (Sentís et al, 2025). Our study thus tested whether morphological and physiological differences between native and invasive populations align with expectations based on environmental variation in ambient temperature and the enemy-release hypothesis.

Methods

Study sites and captures

We conducted fieldwork at three different sites. The site within the native range of common waxbills was located at the Darvill Wastewater Treatment Plant (-29.60, 30.43) in Pietermaritzburg, South Africa, where sampling took place from September to November 2022. The other two sites in the invaded range were located in Portugal. The northern site was near Caminha (41.85, -8.80), and the southern site was near Estômbar (37.17, -8.49), and we conducted the fieldwork from June to July 2022. During the fieldwork, the mean temperature in the South African site was 19.46 ± 1.22 °C. In Portugal, the mean temperature in the northern site was 16.9 ± 0.9 °C. In the southern site, the mean temperature was 26.1 ± 3 °C (Fig. 1).

We captured common waxbills in all sites using 12 m mist nets with 16×16 mm mesh (Ecotone) after we lured them with recordings of their vocalisations. We weighed each common waxbill to the nearest 0.1 g. Morphological measurements were taken by two observers. For tarsus length, both observers independently measured the same birds; we assessed inter-observer consistency using linear mixed-effects models and found no significant observer effect. For wing and tail lengths, which were each measured by a single observer per bird, we similarly detected no statistically significant effect of observer identity. Waxbills with brood patches were released immediately after the morphological measurements and were not included in the respirometry trials. Captured waxbills were transported to nearby facilities for metabolic measurements, typically within 4 to 12 h of capture. In South Africa, waxbills were transported to the Animal House of the University of KwaZulu-Natal, Pietermaritzburg, where they were housed in outdoor aviaries (1×3×2 m) with perches and shelter from sun and rain. Food and water were available ad libitum. In Portugal, up to seven waxbills per day were placed in cages (35×29×23 cm) with two birds per cage and ad libitum

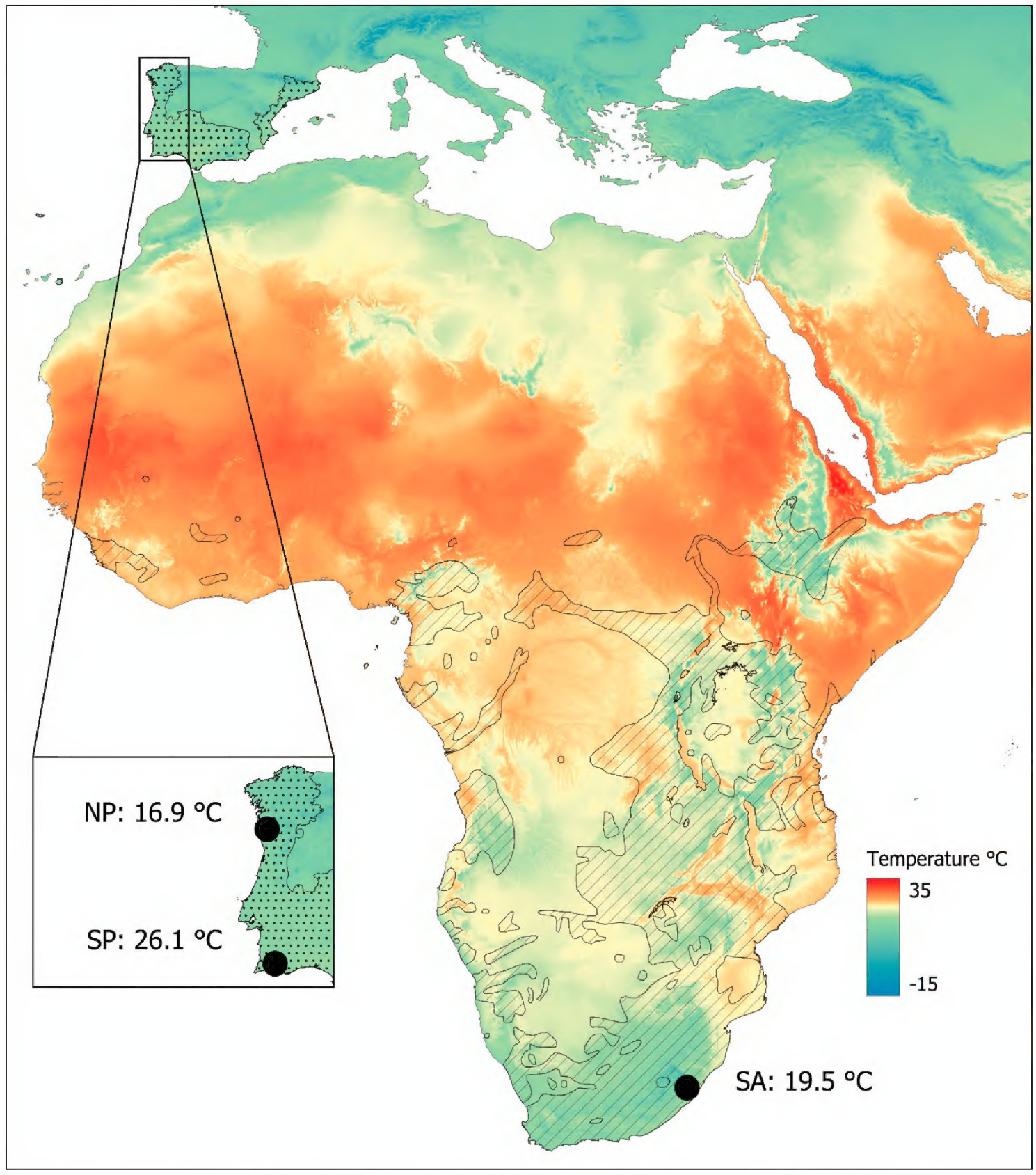

Figure 1. Annual average temperature map (1981–2010) with common waxbill distribution in the native (stripes) and invasive (dots) ranges. (Note: Black circles represent the field sites: NP = northern Portugal, SP = southern Portugal and SA = South Africa. Written temperatures are the mean ambient temperatures during the fieldwork).

access to food (finch mix and millet) and water. After the measurements, waxbills were released at their original capture site. For each common waxbill, if available, two outermost rectrices (tail feathers) were collected for feather analyses (ptilochronology, see below) and molecular sexing. The CHD1-F and CHD1-R primers were used to amplify the CHD1 gene for sexing the birds (Lee et al. 2010). We conducted this research work under ethical permits 'VIB EC2022-090' and 'VIB EC2021-055', as well as SAFRING permit No. '0163', Ezemvelo KZN Wildlife permit 'OP 475', and ICNF Portugal permits N° 256/2021, N° 257/2021 and N° 258/2021.

Basal metabolic rates (BMR)

We used an open flow-through respirometry system measuring O_2 consumption (VO_2; ml/min), CO_2 production (VCO_2; ml/min) and water vapour pressure (kPa) (Field Metabolic System, FMS-3, Sable Systems). To measure basal metabolic rates (BMR), individuals were fasted for 2 h prior to respirometry, and they were then weighed to

the nearest 0.1 g. At sunset, we placed individual waxbills in airtight plastic chambers (1.1 l) and measured their metabolic rate overnight. In South Africa, the chambers were placed inside a temperature-controlled environmental chamber (CMP2244, Conviron, Winnipeg, Canada), and the birds were measured at an ambient temperature of 28 °C, which is within their thermoneutral zone (TNZ) (Pacioni et al. 2023). In Portugal, the birds were placed inside a dark insulating foam box equipped with heating wires and a small fan to maintain an ambient temperature of 28 °C. In both cases, two pumps supplied ambient air, which was divided into separate streams and directed to a mass-flow meter (FB-8, Sable Systems) set to deliver a constant flow of approximately 650 ml/min to each of the eight metabolic chambers – seven housing individual birds and one serving as an empty reference chamber for baseline measurements. Excurrent air from the waxbill and baseline channels were connected to a multiplexer (RM-8 m Sable Systems), which allowed the airstream from one chamber to be sampled independently of the others. The excurrent air from both the bird and baseline channels was alternately subsampled and pulled through the FMS-3, with a subsampling flowrate of 200 ml/min. Waxbills were measured alternately in cycles along with multiple baselines. The time of measurement for each waxbill within a cycle (and the length of each cycle) depended on the number of waxbills within a session. In South Africa, an average of seven birds were measured per night with an average measurement time of 11 h. In Portugal, an average of four birds were measured per night, with a mean measurement time of 9.30 h. We used the software ExpeData (Sable Systems) to record the measurements and extract VO_2 (ml/min) using equation 9.7 from (Lighton 2018). The lowest stable part of the curve (average of 5 min) was selected to estimate BMR overnight. After the measurements, waxbills were weighed again to the nearest 0.1 g and were fed ad libitum. Further information on calibration and respirometry setup can be found in (Pacioni et al. 2023; Sentís et al. 2025).

Body condition

To quantify body condition, we used the Scaled Mass Index (SMI; Peig and Green 2009, 2010), which adjusts individual body mass to the mass that each bird would have if it had a standardised tarsus length. We used a standardised major axis (SMA) regression of log(body mass) on log(tarsus length) to estimate the scaling exponent b (Peig and Green 2009). The SMA regression yielded an estimated slope of 2.01, which was used as the scaling exponent. The mean tarsus length (14.09 mm) was used as the reference length. Following Peig and Green (2009, 2010), we calculated the SMI for each individual (i) as: $\text{body mass}_i \times (14.09/\text{tarsus length}_i)^{2.01}$.

Nutritional condition

We conducted feather analyses to determine the nutritional condition of common waxbills in the three locations. The measurements included feather growth bar widths (GBW), feather density, and feather fault bars. Growth bars consist of alternating dark and light bands on feathers, with each pair reflecting 24 h of growth (Grubb and Cimprich 1990). In cases of severe malnutrition, high energy expenditure, or a combination of both, birds may have to slow their feather growth, which is reflected in narrow growth bars (Grubb 1991). We attached each feather to a white paper marked with a calibration line and fixed them to a polystyrene board to measure the growth bar width of the two outermost tail feathers. The visible

growth bars were marked at their distal and proximal ends along the rachis of the feather using an ultrafine mounting pin (Salleh Hudin et al. 2016; Møller and Nielsen 2018; Gebremichael et al. 2019). Each growth bar's total feather length and width were measured by scanning each paper and using an image analysis script coded in Python. The mean growth bar width was calculated by summing all widths and dividing by the total number of visible growth bars.

Feather density reflects the amount of material invested in feather production during moult (De La Hera et al. 2010a). Reduced feather density may indicate a nutritional deficit during feather growth, as nutritional stress is associated with a lower density of structural elements (Murphy et al. 1988). Feather density has been widely used as a proxy for feather quality because it reflects the balance between lightweight structural efficiency and durability (Butler et al. 2008). Since tail feathers experience substantial mechanical stress during flight, individuals investing less in feather density may suffer higher rates of wear and breakage, which could affect overall fitness (De la Hera et al. 2010b). To determine feather density, we weighed the feathers using an analytical balance (± 0.0001 g), and their length was measured using ImageJ (cm). Feather density was calculated by dividing feather mass by the feather length (mg/cm). The percentage of individuals with fault bars, which are narrow and translucent bands caused by adverse and stressful conditions during feather growth, was recorded for each location.

Statistical analyses

We conducted statistical analyses using the R software v. 4.3.2 (R Core Team 2023). Whole-body BMR and body mass were log-transformed prior to analysis. We used linear regression models to evaluate differences in BMR, body condition and nutritional condition between locations. Independent variables included location (South Africa and southern and northern Portugal), and sex. To account for differences in body size, BMR was analysed as mass-independent by including log-transformed body mass as a covariate in the BMR models. Only adult birds were included in the analyses, as no juvenile birds were caught in South Africa. Equivalence testing was used to assess whether mass-independent BMR from birds in South Africa and northern Portugal were similar. We conducted this analysis calculating the Bayes Factor (BF_{01}) using the 'baymedr' package in R. The Bayes factor compares the likelihood of the data under the null hypothesis (H0, indicating equivalence) against the likelihood under the alternative hypothesis (H1, indicating difference beyond the equivalence margin). When the Bayes factor is greater than 1, the data are more likely to support H0 over H1. Conversely, when BF_{01} is less than 1, the data are more likely to support H1 over H0 (Linde and van Ravenzwaaij 2023). Post-hoc comparisons between locations were conducted using the emmeans function in the 'emmeans' package (Lenth et al. 2018). We conducted a principal component analysis (PCA) to assess size differences, using the wing length, tail length, and tarsus length measurements. The first component of the PCA was then used as a response variable in a linear model to determine size differences between locations.

Results

We measured basal metabolic rate in 98 adult common waxbills, 40 in South Africa, 16 in northern Portugal and 42 in southern Portugal. (Log) body mass and (log) BMR were positively correlated ($r = 0.3$, $p < 0.001$). As expected based on prevailing

ambient temperatures, mass-independent BMR was similar between individuals in South Africa and northern Portugal (BF_{01} = 4.35), and significantly higher than in southern Portugal (NP vs SP: p = 0.03; SA vs SP: p = 0.01; Fig. 2A, Table 1).

Contrary to expectations based on the enemy release hypothesis, body condition, feather density, and body size were not consistently higher in the invaded than in the native range. No significant differences in body condition were detected between locations (p > 0.05; Fig. 2B, Table 1). Feather density was significantly higher in South Africa compared with both northern and southern Portugal (SA vs SP: p < 0.0001; SA vs NP: p < 0.0001; NP vs SP: p = 0.98; Fig. 2C, Table 1). No significant differences were found between locations for GBW (p > 0.05; Suppl. material 1: fig. S2) and feather fault bars, although South Africa had a lower percentage of birds with feather fault bars (p > 0.05; Suppl. material 1: table S1). Regarding common waxbills' size measurements, the first axis of the PCA accounted for 73.3% of the total variance. PC1 scores were: wing length (-0.85), tail length (-0.88), and tarsus length (-0.66). Common waxbills from Portugal were significantly smaller than those from South Africa (NP and SP vs SA, p < 0.0001; Fig. 2D, Table 1).

Sex differences were absent in BMR, body condition, and feather density. However, males exhibited significantly narrower GBW compared to females (p < 0.01), and females were significantly smaller than males (p < 0.0001; Suppl. material 1: table S2).

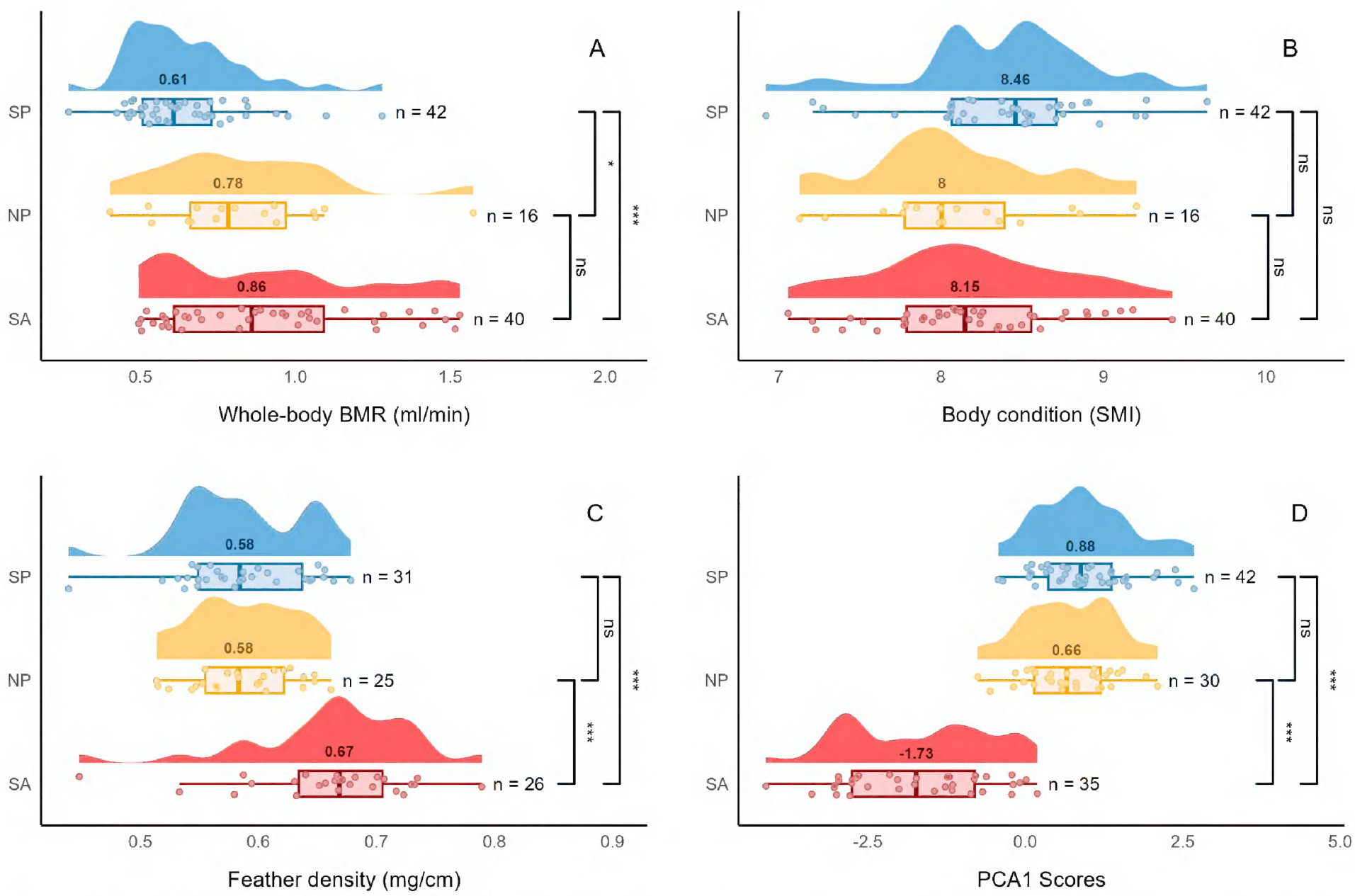

Figure 2. Whole-body BMR (**A**), note that statistical models include body mass as a covariate; body condition (**B**); feather density (mg/cm) (**C**); PCA 1 scores for common waxbill size measurements (wing length, tail length, and tarsus length) (**D**) of common waxbills in southern Portugal (SP), northern Portugal (NP) and South Africa (SA). (Note: n = number of measured individuals. Stars indicate significant differences between locations. *** p < 0.001; ** p < 0.01; * p < 0.05; ns: not significant).

Table 1. Mean (± SD) values of body mass, basal metabolic rate (BMR), Scaled Mass Index (SMI), tarsus length, wing length, tail length, feather density and feather growth bar width (GBW) for common waxbills across three locations: southern Portugal (SP), northern Portugal (SP) and South Africa (SA).

	Location		
	SP	**NP**	**SA**
Body mass (g)	8.08 ± 0.50	8.10 ± 0.50	8.60 ± 0.43
BMR (ml/min)	0.65 ± 0.19	0.83 ± 0.28	0.90 ± 0.33
SMI (g)	8.38 ± 0.55	8.1 ± 0.56	8.18 ± 0.57
Tarsus (mm)	13.8 ± 0.30	14.1 ± 0.35	14.4 ± 0.40
Wing (mm)	47.8 ± 1.12	47.5 ± 0.85	49.8 ± 1.33
Tail (mm)	47.3 ± 1.38	47.3 ± 1.53	53.3 ± 2.73
Feather density (mg/cm)	0.59 ± 0.05	0.59 ± 0.04	0.66 ± 0.07
Feather GBW (mm)	0.47 ± 0.04	0.45 ± 0.03	0.45 ± 0.05

Discussion

This study assessed mass-independent basal metabolic rate (BMR), proxies of body and nutritional condition, and body size of common waxbills, both in their native and invasive ranges. As expected, based on the prevailing temperatures in our study sites, mass-independent BMR was lower in warmer southern Portugal compared to South Africa and northern Portugal, with no significant differences between the latter two. However, contrary to our predictions based on enemy release, body condition was similar in the three locations, while feather density was significantly higher in South Africa. Birds in Portugal were also smaller than those in South Africa. These combined results challenge the often-held notion that species in their invaded ranges exhibit enhanced performance or condition.

Variability in metabolic rates

Our study found that common waxbills in sites with comparable climatic conditions exhibited similar metabolic rates, with lower metabolic rates observed in the warmest region, southern Portugal. This finding suggests the presence of phenotypic plasticity in BMR, and challenges the traditional view that animals of (sub)tropical origin would exhibit minimal physiological plasticity because of the relatively stable climatic conditions in which they evolved (Bozinovic et al. 2011; Naya et al. 2015). Instead, our results align with a more contemporary perspective, asserting that the physiology of tropical birds may be more flexible than previously thought (Pollock et al. 2019). Such plasticity may be attributed to the direct influence of ambient temperatures, where birds adjust the size of their body organs to meet increased thermoregulatory demands (Williams and Tieleman 2000; Zheng et al. 2008; Liknes and Swanson 2011), resulting in changes in maintenance energy requirements (Williams and Tieleman 2000; Zheng et al. 2008). Additionally, alternative drivers, such as non-temperature climate variables, including precipitation, may also significantly influence metabolic rates, e.g. through their effects on habitat quality or food availability (Maldonado et al. 2012). If these variables correlate with ambient temperature, the associations we have observed between BMR and ambient temperature could be indirect.

Phenotypic plasticity in BMR has been associated with the ecological success of species (Katz and Naug 2020; Glazier and Gjoni 2024). Specifically, species that encounter greater climatic variability often demonstrate wider physiological tolerances and, consequently, are capable of occupying larger geographical ranges than

related species from more stable climates (Stevens 1989; Khaliq et al. 2014; Sun et al. 2022). Common waxbills thrive across a broad range of habitats from Ethiopia to South Africa, encompassing various climatic conditions (Péron and Altwegg 2015). To ascertain whether the lower metabolic rates observed in southern Portugal represent a novel phenotype (sensu Levis et al. 2022) or fall within the variability seen in their native range, it is necessary to conduct comparative studies along climatic gradients within the native range, or at least within the range of the likely source population for the invasive Portuguese birds. Future research should also aim to determine whether the patterns in BMR found here reflect adaptive phenotypic plasticity or is instead a consequence of non-adaptive processes (e.g. founder effects and genetic drift) (Ghalambor et al. 2007; Dlugosch and Parker 2008).

Similarly, there is ongoing debate about the extent to which BMR is causally linked to functional metabolism, with studies arguing that such relationships are more likely phenotypic rather than causal (Swanson et al. 2012; Norin and Metcalfe 2019). Nevertheless, BMR remains widely used in physiological ecology as a key indicator of animal energetic strategies (Briscoe et al. 2023; McGrosky and Pontzer 2023), and we here adopt the framework of Kearney et al. (2021), which defines functional traits as those influencing survival, development, growth, and reproduction through their role in an organism's energy balance and environmental interactions. In this context, BMR serves as a key physiological trait that reflects how individuals adjust their metabolism to different thermal environments (Rezende and Bacigalupe 2015; Swanson et al. 2017). Our findings highlight the importance of accounting for intraspecific variability in BMR, for example, when developing mechanistic ecophysiological models to predict invasion risks (Strubbe et al. 2023). In such models, metabolic rates are used as proxies for an animal's capacity to generate heat and maintain homeothermy (Briscoe et al. 2023).

Body and nutritional condition

Contrary to our prediction derived from the enemy release hypothesis, common waxbills in Portugal showed a similar body condition to that of native populations in South Africa. This suggests that other ecological factors in the invasive range, such as novel parasites, intraspecific competition, or resource trade-offs, may offset the benefits of enemy release. While waxbills in Portugal are not affected by, for example, their primary brood parasite, the pin-tailed whydah (*Vidua macroura*), they may still be susceptible to other parasites. Invasive species may be free from enemy pressure only during the initial phase of invasion (Flory and Clay 2013). For instance, Kołodziej-Sobocińska et al. (2018) found that infection intensity by gastrointestinal parasites of invasive American mink (*Neogale vison*) increased over time since their introduction, negatively affecting the minks' body condition. Additionally, although Portuguese waxbills often exploit human-modified habitats like rice fields where the interspecific competition is reduced (Batalha et al. 2013; Sullivan et al. 2015), they may be subject to increased intraspecific competition if population densities are higher (Choquenot 1991; Marra et al. 2015; Lamb et al. 2017). Furthermore, while abundant resources can support higher body condition (Brown and Sherry 2006; McNab 2010), predictable resources might lead to a trade-off in which birds maintain a lower body mass to enhance escape performance from predators (Macleod et al. 2008). Without empirical data on food availability or population densities in both ranges, isolating these factors remains challenging. Our findings emphasize the complexity of invasion ecology, indicating that enemy release benefits, even if present, can be outweighed by other mechanisms.

Whereas body condition indicates an animal's overall condition at the moment of capture, and thus provides a snapshot view, feather-based proxies integrate animal conditions over a longer time frame, namely the period of feather growth during moult, which is an energetically demanding process (Cyr et al. 2008). A poor quality plumage usually represents a reduced investment in feather growth at the benefit of other traits that are essential to fitness, such as the immune system (Sanz et al. 2004; Martin 2005; Moreno-Rueda 2010), and only individuals with a good condition may exhibit both (Moreno-Rueda 2010). However, feather GBW, feather density and the prevalence of fault bars do not suggest that invasive birds are generally in better condition. On the contrary, South African birds exhibited denser feathers than their counterparts in Portugal and also tended to have fewer feather fault bars. When faced with energetic constraints during moult, birds may opt to maintain feather growth rates (Strochlic and Romero 2008; DesRochers et al. 2009) because of the flight inefficiencies associated with feather growth (Echeverry-Galvis and Hau 2013). Our results indicated that individuals from native and invasive populations have similar feather growth rates (i.e. GBW). However, this comes at the expense of lower feather quality in the latter, suggesting that common waxbills may experience energetic trade-offs in their invasive range. This could mean that the species may struggle to cope with the additional energy demands of colder and drier habitats during energetically demanding conditions, and this may reduce their potential for further range expansion into such areas. However, it should be noted that tail moult strategies in common waxbills may vary among populations (Vowles and Vowles 1987), suggesting the need for careful consideration without information on precise moult timing.

Size differences

Contrary to expectations, South African common waxbills were larger, not smaller, than invasive waxbills. While this result aligns with the feather-based condition proxies, suggesting that environmental conditions allow birds in the native range to grow larger and attain better plumage quality, care should be taken because of known size differences between common waxbill subspecies in their native range (del Hoyo et al. 2010). Cardoso et al. (2014) genotyped common waxbills from Portugal and found that they have mixed subspecies ancestry, and most likely descend from birds introduced from former Portuguese colonies such as Mozambique and Angola (Cardoso and Reino 2018). To help interpret whether the size differences between South African and Portuguese common waxbills found here can arise because of introduction history rather than from differing environmental pressures, we also analysed size data from birds originating from past Portuguese colonies and compared them with data from South African birds (Suppl. material 1: figs S3, S4). The analysis showed that subspecies from Portuguese colonies are generally smaller than their South African counterparts but similar to birds from Portugal. Therefore, it is possible, or even likely, that the observed size differences between the two sites are not due solely to ecological factors.

Study limitations

A limitation of our study is that we sampled only two populations in the invasive range and a single population in the native range, which limits our ability to determine whether the observed differences are because of native versus non-native status, other sources of population-level variation, or adaptive processes. Moreover,

for most of our phenotypic proxies, differences between ranges were minor. Only feather density differed significantly, with an 11% difference between locations. While similar studies suggest that even subtle differences in feather traits can influence condition (e.g., Carbonell and Tellería 1999), the magnitude is relatively small (~10% coefficient of variation) and comparable to intraspecific variation reported in other studies (e.g. Catfolis et al. 2023). Consequently, the ecological significance of these differences remains uncertain and should be interpreted cautiously. Additionally, feather density estimates may have been influenced by factors such as feather wear and abrasion, introducing inherent uncertainty into analyses based on feather measurements (Terrill and Shultz 2023). Future studies could consider integrating neutral genetic marker analyses with common garden experiments across climatic gradients to help clarify the relative contributions of adaptive versus non-adaptive processes (e.g. Keller and Taylor 2008; Mühlenhaupt et al. 2021) in explaining invasion success. Another potential limitation is that birds in South Africa were housed in outdoor aviaries, while those in Portugal were kept in smaller cages during measurements. Although all birds had ad libitum access to food and water, differences in housing conditions could have influenced stress levels and metabolic rates. Future studies should standardise housing conditions to minimise potential artefacts and better isolate the effects of environmental variation and introduction history.

Conclusions

Our study showed that common waxbills exhibit considerable plasticity in their basal metabolism, with lower metabolic rates observed in warmer southern Portugal, supporting our hypothesis that ambient temperature is associated with variation in BMR, challenging previous notions of limited plasticity in (sub)tropical birds. However, the lack of body condition differences between native and invasive populations challenges the enemy release hypothesis, suggesting that reduced predation or parasitism in the invasive range does not enhance performance in common waxbills. Instead, invasive waxbills may face compensatory trade-offs, as evidenced by their lower feather density and hinting that the novel environment imposes a cost that could hinder further expansion. The observed size differences between populations are more likely to be of anthropogenic origin, resulting from the selective introduction of birds from the Portuguese colonies. Our results highlight the potential energetic and morphological constraints shaping the waxbills' invasive range.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

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Data availability

The data underpinning the analysis reported in this paper are deposited in Figshare at: https://doi.org/10.6084/m9.figshare.26152504.v2.

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Supplementary material 1

Supplementary information

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